Diet and habitat of Siwalik primates *Indopithecus*, *Sivaladapis* and *Theropithecus*

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We present dental enamel stable carbon and oxygen isotope data, histological analyses of daily cross striations and perikymata, and microwear data of Late Miocene primates *Indopithecus* and *Sivaladapis nagrii* and an early Pleistocene primate *Theropithecus delsoni*, known from the Indian Siwaliks. The results indicate that the Late Miocene giant ape *Indopithecus* had a C_3 diet, likely including nuts, seeds and fruits with hard cover, and most probably lived in a seasonal forest that experienced long dry and wet seasons. While the seasons changed as depicted by intra-annual variation in $\delta^{18}O$ values, the C_3 component of diet was similar throughout the year, as indicated by consistent $\delta^{13}C$ values. *Sivaladapis nagrii* dental enamel $\delta^{13}C$ and $\delta^{18}O$ values, striations and pit percentages indicate that this small primate (3 kg) was a C_3 mixed folivore-frugivore. *Theropithecus delsoni* dental enamel $\delta^{13}C$ and $\delta^{18}O$ values and microwear pattern indicate a diet comprising mainly C_4 grasses or sedges.

Introduction

Indopithecus giganteus (or *Gigantopithecus bilaspurensis*) was an ape the size of a female gorilla (150+ kg, Fleagle 1999) that lived in the sub-Himalayan Siwaliks of India and Pakistan, in the Late Miocene from ca. 8.6 to 8.85 Ma ago (Pillans *et al*. 2005). The genus *Indopithecus* was erected by Von Koenigswald (1950) based on an unusually large isolated molar (GSI D-175) recovered from Alipur, now in Pakistan, which had been described as *Dryopithecus giganteus* by Pilgrim (1915). Subsequently, the same specimen was allocated to *Dryopithecus* (*Sivapithecus*) *sivalensis* by Simons and Pilbeam (1965), who considered this specimen to be similar to *Sivapithecus*. The discovery of a mandibular specimen (CYP359/68) from Haritalyangar, India, and its similarity to those of the Chinese Pleistocene giant ape, *Gigantopithecus blacki*, led Simons and Chopra (1969) to propose a new species, *Gigantopithecus bilaspurensis*. However, Cameron (2001, 2003), based on his studies on functional morphology and phylogenetics, argued that the mandibular specimen should be reallocated to the species *Indopithecus gigan-*

teus. Szalay and Delson (1979) and Wolpoff (1999) were of the opinion that *Indopithecus* was a "thick enameled ground ape". Pillans *et al*. (2005) described an isolated tooth of *Indopithecus* (HDI-1) from Haritalyangar (Fig. 1A and B), India, which has been studied here for stable isotope, dental microstructure, and microwear analyses.

Sivaladapis was a small late-Miocene primate, weighing around 3 kg (Fleagle 1999) and belonging to the adapoid family Sivaladapidae. Early sivaladapids, including *Hoanghonius*, *Rencunius*, *Guangxilemur* and *Wailekia* appeared in the Middle Eocene of China and Thailand (Woo & Chow 1957, Gingerich *et al*. 1994, Ducrocq *et al*. 1995, Tong 1997, Qi & Beard 1998, Gebo *et al*. 1999, Tong *et al*. 1999), and sivaladapids have also been reported from the Eocene of Myanmar (e.g. Beard *et al*. 2007). In the Oligocene deposits, *Guangxilemur* occurs at Bugti Hills, Pakistan (Marivaux *et al*. 2002). During the Miocene, the sivaladapids were taxonomically and geographically very diverse with *Sivaladapis* and *Indraloris* from southern Asia, *Sinoadapis* from China, and *Siamoadapis* from Thailand (Lewis 1933, Tattersall 1968, Prasad 1970, Gingerich & Sahni 1979, 1984, Thomas & Verma 1979, Wu & Pan 1985, Pan & Wu 1986, Pan 1988, Sahni 1989, Barry *et al*. 2002, Pillans *et al*. 2005, Flynn & Morgan 2005, Chaimanee *et al*. 2008). By the end of the Miocene sivaladapids became extinct (Gingerich & Sahni 1984). The three sivaladapid specimens, Hari I-6, Hari I-7 (Pillans *et al*. 2005) and P11 (Gingerich & Sahni 1984) studied here come from Dhok Pathan Formation, Haritalyangar (Fig. 1A and B).

One mandibular fragment of the papionin cercopithecine, *Theropithecus delsoni* (A643), is known from the locality of Mirzapur, near Chandigarh (Fig. 1C) (Gupta & Sahni 1981, Delson 1993, Delson *et al*. 1993). Its age is tentatively considered ~1 Ma (Pinjor Formation) as the specimen does not come from a well dated section (Patnaik & Nanda 2010). The presence of *Theropithecus* in India holds significance as it is considered that *Homo erectus*, *Theropithecus*, *Megantereon whitei*, and *Hippopotamus* were among the first mammals to disperse out of Africa in the early Pleistocene (Martinez-Navarro 2004, Rook *et al*. 2004, Fleagle *et al*. 2010).

Mammalian dental enamel contains periodic growth structures that preserve the history of development of the tooth. Each sub millimeter tooth enamel increment (perikymata) is secreted in 8 days in *Sivapithecus indicus*, and 9 days in *Sivapithecus parvada* (Mahoney *et al*. 2007). In *Gigantopithecus blacki* the periodicity has been found to be 11 days per perikymata (Dean & Schrenk 2003). *Graecopithecus*, a large-bodied Miocene ape from Greece, which has been considered phylogenetically closer to *Indopithecus* (Gelvin 1980, Cameron 2001), has a periodicity of 8 days (Smith *et al*. 2004). Among the extant apes, *Hylobates lar* which weighs around 6 kg, shows a periodicity of 4 days (Dirks & Bowman 2007); *Pan troglodytes* (33–45 kg) has a periodicity of 6 to 7 days (Smith *et al*. 2003); *Gorilla* (98–163 kg) has a periodicity of 7 to 10 days; *Pongo* (36–78 kg) has a periodicity of 8–11 days (Schwartz *et al*. 2001, Hu *et al*. 2011). Hence, it appears that there is a positive correlation between periodicity and body mass in hominoids (Reid *et al*. 2002, Hu *et al*. 2011).

Tooth enamel bioapatite of extant and fossil species preserves a record of carbon and oxygen isotopes incorporated through ingested food and water. In most tropical and many subtropical ecosystems, the carbon isotope composition ($\delta^{13}C$) of tooth enamel in modern herbivores distinguishes between diets dominated by C_3 plants (dicots including trees, shrubs, herbs, forbs; and cool season (high latitude or altitude) grasses or sedges), and those dominated by C_4 plants (mostly monocots, such as warm-season grasses and sedges); mixed-feeding comprises a mixture of C_3 and C_4 plants (Lee-Thorp & Van der Merwe 1987, Bocherens *et al*. 1996, Cerling *et al*. 1997). Enamel is enriched in ^{13}C by 12‰ to 14‰ with respect to diet (Cerling & Harris 1999, Passey *et al*. 2005). For the post-Miocene, interpretations of C_3 *vs*. C_4 diets of extinct mammals are based upon certain cut-off values of $\delta^{13}C$ in dental enamel. For instance, the $\delta^{13}C$ values from dental enamel representing a pure C_3 diet of a modern mammal would range from approximately –20‰ to –8‰, with the most negative values indicating a diet from the ground-level of closed canopy rainforest, and the higher values indicating a C_3-diet derived from an open habitat, which could range from open forest or woodland
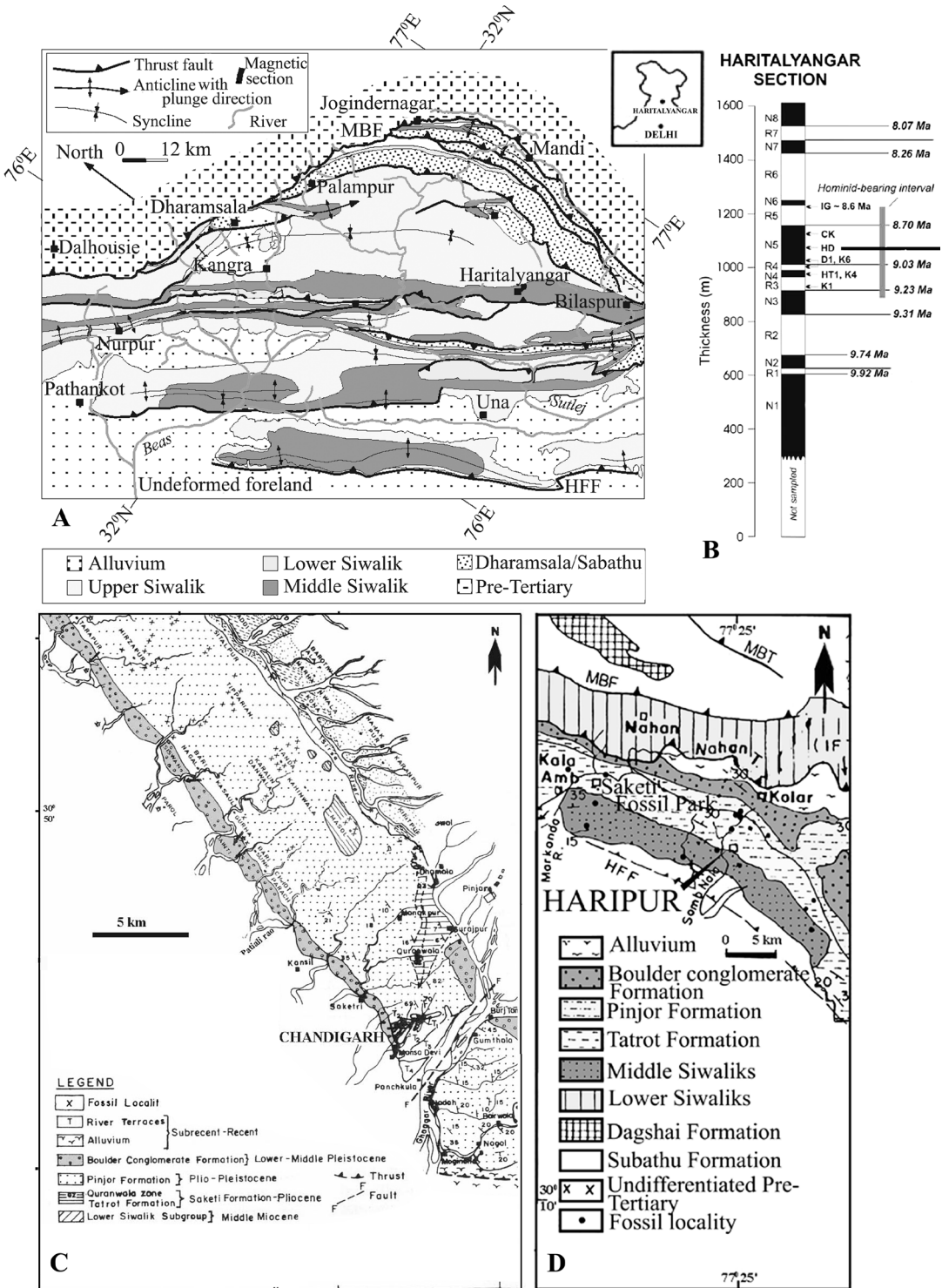
Fig. 1. (**A**) Location of the Himachal Pradesh reentrant [modified from Brozovic & Burbank (2000)]. (**B**) Magneto-stratigraphic section at Haritalyangar (after Pillans *et al.* 2005). (**C**) Fossil localities in the vicinity of Chandigarh [modified from Sahni & Khan (1964)]. (**D**) Area around Haripur situated 100 km east of Chandigarh [modified from Kumar *et al.* (2002)].
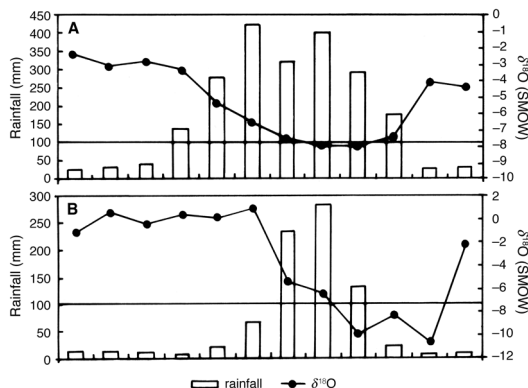
Fig. 2. Monthly (January–December) rainfall amount and $\delta^{18}O$ (SMOW) values illustrating the amount effect for (**A**) Hong Kong and (**B**) New Delhi, (modified from fig. 5 of Nelson 2005, reproduced with permission from Elsevier).

to grassland (Cerling *et al.* 1997, Cerling *et al.* 2004). On the other hand, a pure C_4 diet would yield $\delta^{13}C$ (enamel) values between +1‰ to +4‰. Prior to the late Miocene, most ecosystems on Earth were dominated by C_3 plants so that the modern C_3-browsing/C_4-grazing distinction cannot be used for these older periods of time.

The oxygen isotope ratio of dental enamel depends upon body water, which is derived from drinking water, water in plants, and metabolically derived water (Kohn 1996, Kohn *et al.* 1996, Sponheimer & Lee-Thorp 1999). Differing proportions of these components, including intake of O_2 and loss of CO_2 and water vapour, determines the $\delta^{18}O$ of body water which, in turn, determines the $\delta^{18}O$ of tooth enamel (Luz & Kolodny 1985, Podlesak *et al.* 2008, 2012, O'Grady *et al.* 2010, 2012). Drinking water is generally derived from meteoric waters, which often show a seasonal cycle; in the monsoon region of Indo-Pakistan, summer precipitation is depleted in ^{18}O as compared with winter precipitation (e.g., Fig. 2) due to the "amount effect" (Dansgaard 1964, IAEA 1981). "Food water" is derived from leaves, which is significantly enriched in ^{18}O relative to its source water. Metabolic water is derived from the oxygen bound in foods (e.g., CH_2O) which is released during respiration by reaction with atmospheric oxygen. The isotopic ratio of drinking water, and the relative proportions of the three water input sources, are both likely to change over seasonal cycles; thus, it is not pos-

sible to determine if ^{18}O-enriched tooth enamel is associated with "dry" or "wet" seasons without *a priori* assumptions or information. However, significant annual variations in body water are likely to indicate high seasonality in the isotope ratios or the relative proportions of these different water sources. Several studies have shown that intra-tooth variation in oxygen isotopic composition of both modern and fossil mammalian taxa provides information on intra-annual seasonal variation (Koch *et al.* 1989, Bryant *et al.* 1994, 1996, Fricke & O'Neil 1996, Fricke *et al.* 1998, Cerling & Sharp 1996, Sharp & Cerling 1998, Gadbury *et al.* 2000, Fox & Fisher 2001) but it is often difficult to extrapolate this directly to seasonal amplitude in the isotopic ratio of local precipitation.

Research on dental microwear patterns (percentage and width of pits and striations) of modern primates has been used to infer dietary preferences of their extinct counterparts (Grine & Kay 1988, Ungar 1996, Merceron *et al.* 2005). Several comparative studies using pit and striation ratios in modern apes such as *Gorilla*, *Pan* and *Pongo* and extinct apes/hominids (e.g., *Sivapithecus*, *Gigantopithecus*, *Paranthropus*, *Australopithecus*) have provided useful information about their diet (Teaford & Walker 1984, Daegling & Grine 1999, Nelson 2003, Ungar *et al.* 2008, Grine *et al.* 2009). It also permits understanding interspecific dietary differences and diet variation linked to seasonal and ecological factors (Teaford 1986, Teaford & Oyen 1989, Teaford & Robinson 1989, Teaford & Glander 1996). As such, it is the abrasive component associated with food that is responsible for the formation of pits and scratches. A low percentage of pits on wear facets is interpreted to indicate folivory, whereas a high percentage of pits indicates a fruit dominated diet. A high percentage of long, wide parallel oriented scratches indicate a grazing habit. Primates that eat a lot of hard food such as seeds, nuts and roots have very high number of pits, large pits and wide scratches (Ungar 1996, King *et al.* 1999). However, one should be careful while making such interpretations, as post-mortem changes prior to the final burial (taphonomic modifications) of the samples may lead to formation of similar scratches and pits (Ungar *et al.* 2006). To reconstruct dietary behaviour of small primates, body mass and shearing quotients (SQ) are also widely

used (Kay 1975, Kay & Covert 1984, Kirk & Simons 2001, Ramdarshan *et al*. 2010). Primates under 350 g obtain protein mainly from insects or other invertebrate fauna, while those above 600 g are usually more herbivorous. Molars of primates that eat insects and leaves have long and sharp crests, while those eating fruits have shorter crests and shallower basins.

Material and methods

This study from the Indian Siwaliks includes the primates *Indopithecus* and *Sivaladapis nagrii* from the Miocene Dhok Pathan Formation, and *Theropithecus delsoni* from the Pleistocene. Paleosol carbonates from the Miocene localities near Haritalyangar were collected from well-developed paleosols using the criteria as described in Quade and Cerling (1995). Associated mammalian fauna collected from Dhok Pathan Formation exposed near Haritalyangar and Upper Siwaliks around Chandigarh region is also included in this study.

Stable isotope analyses

Stable isotope analyses were performed using both conventional H_3PO_4 digestion and laser ablation methods. For conventional analysis of enamel, approximately 5 milligrams of powdered enamel was treated using conventional methods to remove carbonates (Cerling *et al*. 2011); paleosol carbonates required no pretreatment. Samples were reacted with 105% H_3PO_4 at 90 °C and analyzed on an isotope ratio mass spectrometer (IRMS) with results reported in the permil notation:

$$\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000 \qquad (1)$$

where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios for the sample and standard, respectively. An analogous expression is used to report $^{18}O/^{16}O$ ratios. For both $\delta^{13}C$ and $\delta^{18}O$ the isotope standard is V-PDB (Vienna-Pee Dee Belemnite). Fossil isotope reference materials and an acid fractionation factor of 1.00725 were used to correct $\delta^{18}O$ enamel values to 25 °C (*see* Passey *et al*. 2007).
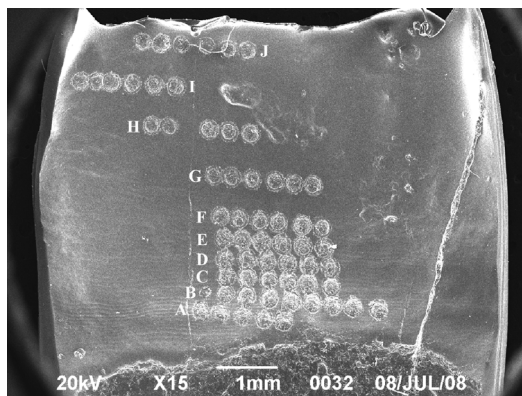

Fig. 3. Laser ablation pits and perikymata on a silicon rubber mould of the *Indopithecus* (HDI-1) molar surface (A–G lateral and H–J cuspal enamel). There are 38 perikymata between samples A and G.

For selected samples, analyses were made using laser ablation (LA) to liberate CO_2 from bioapatite enamel, using the methods of Cerling and Sharp (1996) as modified by Passey and Cerling (2006) (Figs. 3 and 4A). Multiple analyses of a single tooth from the Siwaliks using both methods was used to normalize the LA-IRMS results to the conventional H_3PO_4 results; the offset was 5.1‰ between the two methods for $\delta^{18}O$ results; no correction was applied to the $\delta^{13}C$ values because the offset between the laser and conventional results was similar to the analytical uncertainty (~0.1‰).

Growth periodicity studies

For determining growth periodicity of *Indopithecus* and *Theropithecus* a fractured piece of enamel was removed from the tooth, its transverse surface was cleaned with acetone, and was etched with 5% HCl for 100 seconds. In case of *Sivaladapis*, the removed enamel piece was embedded in polyester resin, its transverse surface was polished, cleaned with acetone and etched with 5% HCl for 80 seconds. The surface was coated with gold palladium and was examined under a scanning electron microscope (JSM JEOL, 6460) at the Geology Department, Panjab University to record the presence of both short- and long-period incremental growth lines in enamel. Short-period lines, or cross-striations,
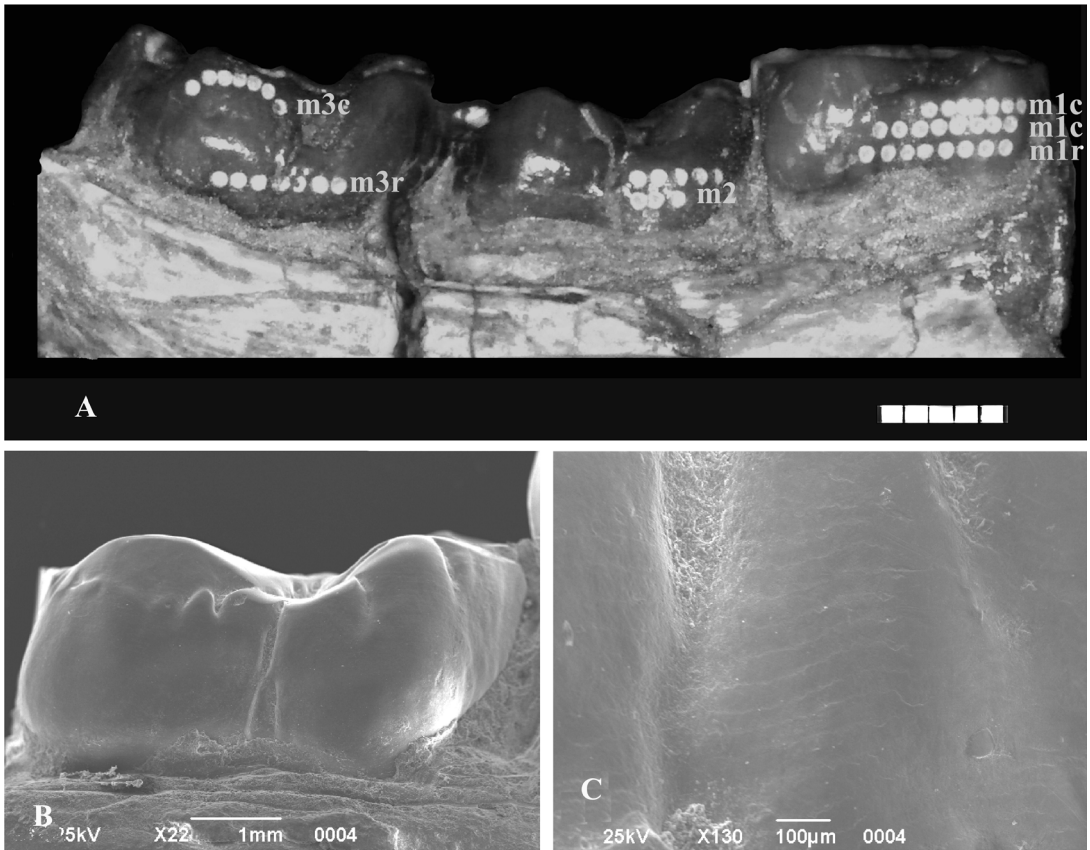
Fig. 4. (**A**) *Sivaladapis nagrii* $M_1M_2M_3$ (P11) with laser scan pits (scale **5** mm). (**B**) SEM image of labial view of *Sivaladapis nagrii* M_1 (Hari I-6). (**C**) a portion of the M_1 magnified to show perikymata.

represent daily increments of enamel deposition. Long-period lines, referred to as Retzius lines or striae of Retzius (manifested on the tooth enamel surface as 'perikymata'), represent periodic disruptions in enamel deposition that occur every six to twelve days in extant great apes and humans, although the periodicity is constant within any given individual (Dean 1987, 1998, 2000, FitzGerald 1998).

Microwear studies

For dental enamel microwear studies, a mould of the *Indopithecus* tooth was prepared using a RTV silicone rubber, followed by the preparation of a cast made by using a polyester resin (Araldite). The semi-transparent cast was surveyed under transmitted light of a Leica S8APO microscope to find areas that were unaltered taphonomi-cally. The cast was then coated with gold palladium and was viewed under SEM. In case of *Sivaladapis* a P4 (Hari I-6) was coated with gold and viewed under SEM for microwear studies. Several images of *Indopithecus*, *Sivaladapis* and *Theropithecus* Phase II wear facets were taken and one from each tooth was selected to count/measure pit percentage, pit width and length and scratch width. To check the reliability and consistency of the microwear pattern, two adjacent areas were scanned at a 500× magnification (*see* El-Zaatari *et al*. 2005 for details). The micrographs were saved as gray-scale image files at 200 dpi resolution and cropped to 640 × 480 pixels. The counts and measurements were made by one observer (RP) using MICROWARE 4.0.2 (Ungar 2002). A comparison of these features was made with those reported in published works on both extant and extinct primates (Walker & Teaford 1989, Rafferty *et al*. 2002, Nelson 2003,

El-Zaatari *et al*. 2005, Merceron *et al*. 2005, Ungar *et al*. 2006, Ramdarshan *et al*. 2010).

Results

Relationship between isotope sampling and growth structures

Stable isotopes measurements in enamel represent an attenuated signal because of maturation of enamel over some period of time (Passey & Cerling 2002). The temporal discussion in this section refers to the crown formation time of enamel, which does not include maturation time. The time interval sampled for isotope analysis includes crown formation time and maturation time; however, the true interval cannot be estimated without a good model for the enamel maturation process in these species.

The right M^2, VPL/HDI (1) of *Indopithecus* from 8.85 Ma and Middle Siwaliks of Haritalyangar (Pillans *et al*. 2005) had 10 laser scans, each comprised of 5–8 ablation pits (Table 1 and Fig. 3). Laser ablation pits were of ~250 μm diameter and the outcropping Retzius lines formed ~50–70 μm thick perikymata. In total

38 perikymata were sampled that represent ~418 days (based on the periodicity of 11 cross-striations per perikymata; Fig. 5) for samples A–G (*see* Fig. 3). Perikymata in scans H–J are not distinct (*see* Fig. 3).

For stable isotope analysis of *Sivaladapis nagrii*, a mandible comprising M_1, M_2 and M_3 (P11) was used (Fig. 4A). A total 6 laser scans (m1c, m1c2, m1r, m2, m3c and m3r) were obtained from the labial face of the three teeth, each scan comprised of 5–8 ablation pits (Fig. 4A). Sivaladapid teeth were too small to sample by traditional drilling methods, so the LA-GC-IRMS method was the only means by which the tooth could be sampled for isotope analysis. Each pit was ~250 μm in diameter. The outcropping Retzius lines formed ~40–50 μm thick perikymata. Therefore, the six scans covered around 30 perikymata on the lateral enamel of the molars of *Sivaladapis nagrii* (Fig. 4B). A growth periodicity of two days (Fig. 6) was estimated using SEM. For such periodicity, isotope data from 6 laser scans of around 30 perikymata would represent approximately a two-month record of diet and climate. We, therefore, did not expect to find a seasonal variation in $\delta^{18}O$ values in the *Sivaladapis nagrii* molars studied here.

Table 1. Stable isotope results from laser ablation. $^{18}\varepsilon_{\text{laser-acid}}$ = −5.1‰ for all $\delta^{18}O$ data. No difference was found between laser and conventional $\delta^{13}C$ data.

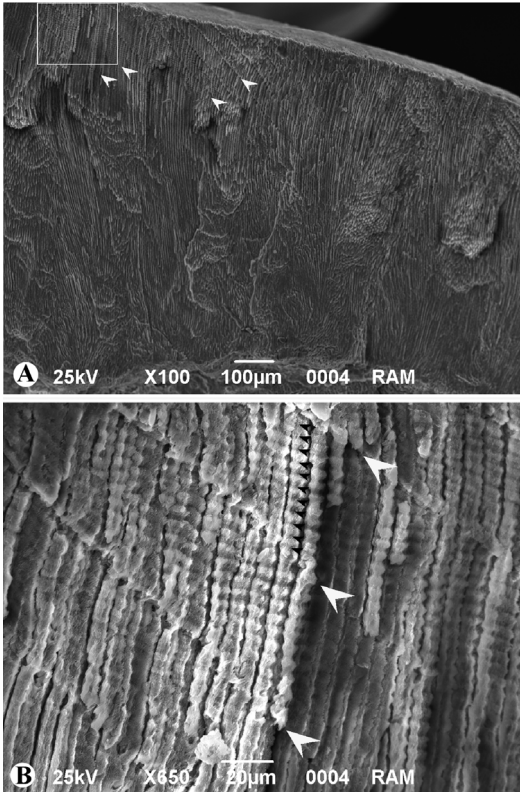|	Distance from the base of the crown (mm)	$\delta^{13}C$	$\delta^{18}O$	
			laser measured	CO$_3$ equivalent
Indopithecus				
HD1-A	0.3	−12.2	−10.6	−5.5
HD1-B	0.6	−11.8	−9.5	−4.4
HD1-C	0.9	−11.7	−7.6	−2.5
HD1-D	1.2	−11.9	−7.2	−2.1
HD1-E	1.5	−11.8	−8.0	−2.9
HD1-F	1.8	−11.6	−8.2	−3.1
HD1-G	2.4	−12.4	−10.3	−5.2
HD1-H	3.0	−12.1	−9.3	−4.2
HD1-I	3.6	−12.2	−10.1	−5.0
HD1-J	4.2	−12.2	−8.7	−3.6
Sivaladapis				
P11_m1c		−11.6	−10.0	−4.9
P11_m1c2		−11.3	−9.4	−4.3
P11_m1r		−12.4	−9.8	−4.7
P11_m2		−12.7	−9.3	−4.2
P11_m3c		−13.4	−9.6	−4.5
P11_m3r		−14.0	−10.1	−5.0

Fig. 5. (**A**) Enamel microstructure as seen in a cross-section on the *Indopithecus* tooth (HDI-1). (**B**) Portion inside the box in **A** magnified. Short-period lines, or cross-striations, representing daily increments of enamel deposition are shown by black arrows. Long-period lines, referred to as Retzius lines or striae of Retzius are shown by white arrows. Arrows point towards the occlusal surface of the tooth.
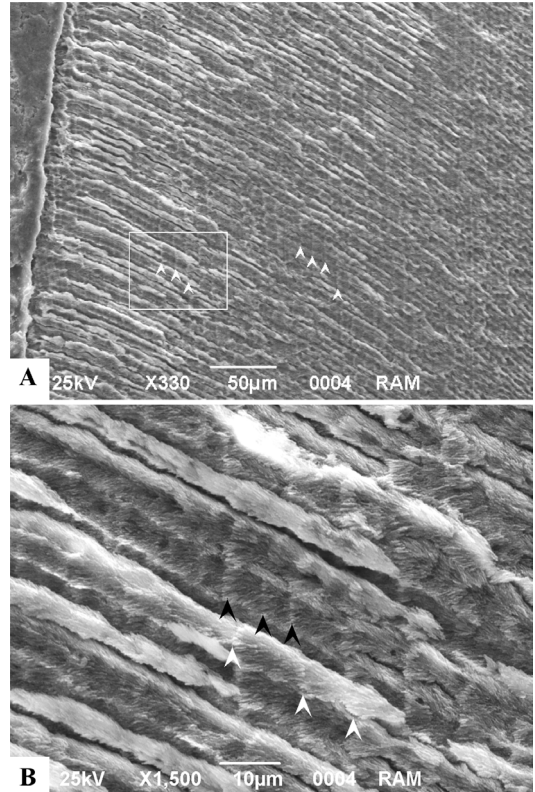

Fig. 6. (**A**) Enamel microstructure as seen in a cross-section on the *Sivaladapis nagrii* M_1 (Hari I-7). (**B**) Portion inside the box in **A** magnified. Short-period lines, or cross-striations, representing daily increments of enamel deposition are shown by black arrows. Long-period lines, referred to as Retzius lines or striae of Retzius are shown by white arrows. Arrows point towards the occlusal surface of the tooth. Enamel surface is towards the left and enamel dentine junction is to the right.

A sample for stable isotope analyses from the *Theropithecus* molar enamel was obtained using a dental drill that covered around 30 perikymata. *Theropithecus* molar enamel microstructure shows a periodicity of 7 days (Fig. 7), therefore carbon isotope data from the drill pit covering 30 perikymata gives an average diet over a period of ca. 7 months.

Stable isotopes in Siwalik primates

The laser scans A–J on the *Indopithecus* tooth (Fig. 3) yielded min, max and mean $\delta^{13}C$ values of –12.4‰, –11.6‰ and –12‰, respectively; and the min, max and mean $\delta^{18}O$ values (adjusted to equivalent enamel-CO_3 values) of –5.5‰ and –2.1‰ and –3.9‰, respectively (Tables 1 and 2). The laser scans (Fig. 4A) of the m1c, m1c2, m1r, m2, m3c and m3r on *Sivaladapis nagrii* teeth yielded min, max and mean $\delta^{13}C$ values of –14.0‰, –11.3‰ and –12.5‰, respectively; and the min, max and mean $\delta^{18}O$ values (enamel-CO_3 equivalent) of –5.0‰, –4.2‰ and –4.6‰, respectively (Table 2).

The $\delta^{13}C$ and $\delta^{18}O$ values for a single sample from *Theropithecus* were –1.9‰, and –2.0‰, respectively (Table 2). For the mean $\delta^{13}C$ and $\delta^{18}O$ values from laser or conventional sampling for Siwalik primates, associated mammalian fauna, and paleosol carbonates *see* Fig. 8.

Paleosol carbonates

The Haritalyangar paleosol carbonate $\delta^{13}C$ values ranged between –12.2‰ (min) and –8.0‰ (max) with mean = –10.8‰ (Table 3 and Fig. 8). Soil carbonate $\delta^{18}O$ values range between –9.2‰ (min) and –5.8‰ (max) with mean = –7.7‰ (Table 3 and Fig. 8).

Stable isotopes of associated fauna

The older Dhok Pathan associated fauna includes bovids, cervids, equids, rhinocerotids, suids and tragulids. The $\delta^{13}C$ values range between –13.2‰ (min) and –10.7‰ (max) with mean = –12.1‰, and the $\delta^{18}O$ between –0.3‰ (min) and –11.9‰ (max) with mean = –5.7‰ (Table 2 and Fig. 8). Associated fauna from younger deposits (1 to 3 Ma) include bovids, camelids, equids, giraffids, hippopotamids, and rhinocerotids with the $\delta^{13}C$ values ranging from –2.9‰ (min) to +2.0‰ (max) with mean = –1.7‰. Elephantids are represented by *Elephas* and *Stegodon*; *Elephas* has the $\delta^{13}C$ values of –0.9‰ (min) and –0.1‰ (max) with mean = –0.4‰, whereas *Stegodon* has min, max and mean $\delta^{13}C$ values of –11.9‰ ,–7.3‰ and –9.4‰, respectively (Table 2 and Fig. 8). $\delta^{18}O$ values of associated fauna from the younger deposits ranges from –7.6‰ (min) to +0.3‰ (max) with mean = –2.8‰.

Enamel microstructure

Lateral enamel of *Indopithecus* shows Rhetzius lines of ~55 μm thick with 11 prism cross-striations representing 11 days (Fig. 5). This gives an enamel secretion rate of ~5 μm per day. In *Sivaladapis nagrii* the rhetzius lines are ~10 μm thick having 2 cross striations, representing 2 days. The enamel secretion rate in *Sivaladapis nagrii* is ~5 μm per day. Enamel microstructure of *Theropithecus delsoni* shows ~35 μm thick Rhetzius lines with 7 prism cross-striations representing 7 days (Fig. 7), with an enamel secretion rate of ~5 μm per day.

Dental enamel microwear on *Indopithecus* tooth (Fig. 9) reveals that the tooth surface is rather rough and heavily pitted with a high per-
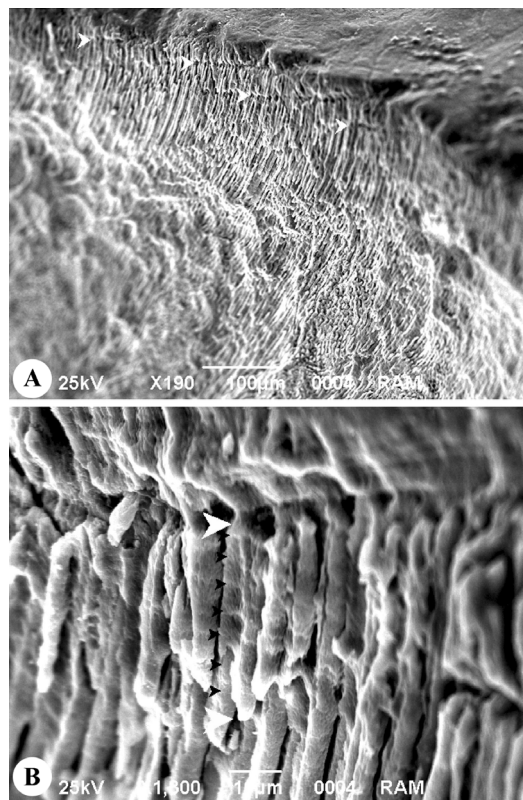

Fig. 7. (**A**) Enamel microstructure as seen in a cross-section on the *Theropithecus delsoni* M_1(A643). (**B**) Part of **A** magnified. Short-period lines, or cross-striations, representing daily increments of enamel deposition are shown by black arrows in **B**. Long-period lines, referred to as Retzius lines or striae of Retzius are shown by white arrows in **A** and **B**. Arrows point towards the occlusal surface of the tooth. Enamel surface is towards the top and enamel dentine junction is towards the bottom.

centage of pits (~58%). The average pit width is 5.57 μm and the average pit length is 8.09 μm. There is a moderate percentage (~42%) of mixed striations present. Striation width and length are on average 2.19 and 36.11 μm, respectively. *Sivaladapis nagrii* dental enamel microwear on grinding lophs (Phase II facets) shows ~60% of small pits and ~40% of long parallel narrow to wide striations (Fig. 9). Pit width averages 1.88 μm. The mean pit length is 2.72 μm. Striation width and length are on average 1.22 and 64.25 μm, respectively. Most of the striations were fine averaging ca. 1 μm, whereas a few are as wide as 5 μm. Few fine cross striations

are also present (Fig. 10). *Theropithecus delsoni* dental enamel exhibits ~34% of small pits and ~66% of fine to wide striations (Fig. 11D). Average pit width is 3.28 μm and average pit length is 4.7 μm. The average width and length of the striations are 1.3 and 22.48 μm, respectively.

Discussion

Indopithecus, Sivaladapis and *Theropithecus* diets and habitats

Indopithecus

The δ^{13}C values for the *Indopithecus* reported

here range from –12.4‰ to –11.6‰, indicating a pure C_3 diet similar to that of the ca. 9.2 Ma *Sivapithecus* from the Siwaliks as reported by Nelson (2007); thus, both *Indopithecus* and *Sivapithecus* had C_3-dominated diets in the Dhok Pathan. A C_3-dominated habitat is supported by the δ^{13}C values obtained from associated *Sivalhippus* and other associated faunal remains, and from soil carbonates from equivalent strata exposed at a nearby site (Kursai 7; Table 2 and Fig. 8). However, because this period represented by the Dhok Pathan sediments is before the global expansion of C_4 ecosystems (Cerling *et al*. 1997), the C_3–C_4 distinction in diets and paleosols cannot be used to evaluate the degree of "openness" of the habitat at this time.

Table 2. Stable-isotope analysis results from mammalian taxa in the Haritalyangar region, Indian Siwaliks. Values in parentheses are averages for samples measured with the laser ablation system (Table 1) with δ^{18}O given as the estimated equivalent value for the CO_3^{2-} component of bioapatite.

Sample ID	δ^{13}C	δ^{18}O	Taxon	Locality	Formation	Age (Ma)
Samples younger than 8 Ma						
M2	–2.9	–2.4	Bovid	Nadah	Pinjor	~1.8
M5	2.0	–1.9	Bovid	Nadah	Pinjor	~2.0
B281	0.0	–3.8	Bovid jaw	Mirzapur	Pinjor	~2.0
KB-1	–2.9	–4.5	Bovid	Kanthro	Tatrot	2.5
PUBMN1	–2.5	0.3	*Camelus*	Moginand	Tatrot	~2.5
DKE-1	–0.1	–5.7	*Elephas*	Devni Khadri	Tatrot	~2.5
F335	–0.3	–3.0	*Elephas*	Quaranwala	Pinjor	1.5
B594	–0.2	–4.0	*Elephas*	Quaranwala	Pinjor	1.8
B246	–0.9	–1.8	*Elephas*	Quaranwala	Pinjor	2.0
A586	–1.7	–3.7	*Equus*	Quaranwala	Boulder Congl.	~1.0
A600	–0.1	–0.1	*Equus*	Mirzapur	Pinjor	~2.0
161-G	–0.4	–0.8	*Hemibos*	Quaranwala	Pinjor	~2.0
F1140	1.9	–7.2	*Hexaprotodon*	Siswan	Tatrot	~2.5
DK1	0.1	–0.8	*Hipparion*	Devni Khadri	Tatrot	~2.5
A565	0.2	–4.5	*Hipparion*	Quaranwala	Pinjor	2.4
B30	0.7	–2.6	*Rhinoceros*	Quaranwala	Pinjor	~1.7
B-276	2.0	–2.0	*Sivatherium*	Quaranwala	Pinjor	~1.7
HPM1	–9.7	–3.8	*Stegodon*	Haripur Khol	Tatrot	2.5
DKS 1	–7.3	–7.6	*Stegodon*	Devni Khadri	Tatrot	~2.5
B-252	–11.2	–4.6	*Stegodon*	Quaranwala	Tatrot	3.0
A643	–1.9	–2.0	*Theropithecus*	Mirzapur	Boulder Congl.	~1.0
Samples older than 8 Ma						
HD1-C	–11.6	–2.7	Bovid	Hari Devi	Dhok Pathan	8.9
D1-1	–10.7	–1.2	Bovid	Dharamsala	Dhok Pathan	10.1
DP8	–13.2	–0.6	Cervid	Chob Ka Nala	Dhok Pathan	8.8
HT1-2	–11.5	–9.6	*Dorcatherium*	HT1	Dhok Pathan	9.1
K1D	–12.5	–3.6	*Dorcatherium*	Kursai-1	Dhok Pathan	9.2
HD1-1 average	(–12.0)	(–3.9)	*Indopithecus*	Hari Devi	Dhok Pathan	8.9
CHK-53	–11.0	–6.3	*Propotamochoerus*	Chob Ka Nala	Dhok Pathan	8.8
DP2	–13.1	–11.9	*Rhinoceros*	Kursai-1	Dhok Pathan	9.2
P11 average	(–12.6)	(–4.6)	*Sivaladapis*	HT1	Dhok Pathan	9.1
CK2	–12.1	–7.4	*Sivalhippus*	Chob Ka Nala	Dhok Pathan	8.8
K1S	–13.2	–7.3	*Sivalhippus*	Kursai-1	Dhok Pathan	9.2
HD 1–4	–12.6	–6.8	*Sivalhippus*	Hari Devi	Dhok Pathan	8.9

Fig. 8. δ^{13}C (VPDB) *vs.* δ^{18}O$_{water}$ (SMOW) values for mammalian teeth and soil carbonates analyzed in this study. The δ^{18}O values for enamel and soil carbonate have been converted from calcite to water using the equation in Kim and O'Neil (1997) assuming temperatures of 37 °C for enamel and 25 °C for soil carbonates.
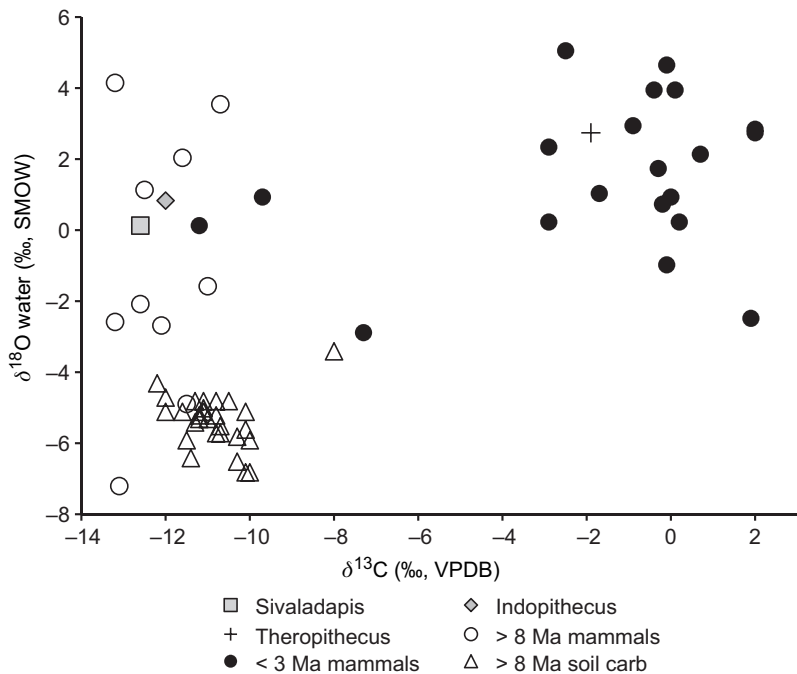

Table 3. Stable-isotope analysis results from paleosol carbonate nodules in the Dhok Pathan Formation, Haritalyangar.

Sample ID	δ^{13}C	δ^{18}O	Locality	Age (Ma)
IN01-HP-301.1	−11.2	−7.6	Kursai-6	9.0
IN01-HP-301.2	−10.8	−8.1	Kursai-6	9.0
IN01-HP-317.1	−11.1	−7.5	Dangar-1	9.0
IN01-HP-317.2	−11.6	−7.5	Dangar-1	9.0
IN01-HP-318.1	−12.2	−6.7	Dangar-1	9.0
IN01-HP-318.2	−11.3	−7.8	Dangar-1	9.0
IN01-HP-319.1	−10.1	−8.0	Dangar-1	9.0
IN01-HP-319.2	−10.0	−9.2	Dangar-1	9.0
IN01-HP-320.1	−10.7	−8.1	Dangar-1	9.0
IN01-HP-320.2	−10.7	−7.9	Dangar-1	9.0
IN01-HP-325.1	−10.3	−8.2	Kursai-6	9.0
IN01-HP-325.2	−10.0	−8.3	Kursai-6	9.0
IN01-HP-326.1	−10.1	−7.5	Kursai-6	9.0
IN01-HP-326.2	−10.5	−7.2	Kursai-6	9.0
IN01-HP-327.1	−8.0	−5.8	Kursai-6	9.0
IN01-HP-328.1	−11.3	−7.2	Kursai-6	9.0
IN01-HP-328.2	−10.8	−7.6	Kursai-6	9.0
IN01-HP-330.1	−11.1	−7.4	Kursai-4	9.1
IN01-HP-330.2	−11.1	−7.2	Kursai-4	9.1
IN01-HP-302.1	−11.2	−7.7	K7	8.9
IN01-HP-302.2	−11.5	−8.3	K7	8.9
IN01-HP-303.1	−11.0	−7.7	Dharamsala	10.1
IN01-HP-303.2	−12.0	−7.5	Dharamsala	10.1
IN01-HP-304.1	−10.8	−7.2	Dharamsala	10.1
IN01-HP-304.2	−12.0	−7.1	Dharamsala	10.1
IN01-HP-306.2	−11.4	−8.8	Dharamsala	10.1
IN01-HP-307.1	−10.3	−8.9	Dharamsala	10.1
IN01-HP-307.2	−10.1	−9.2	Dharamsala	10.1
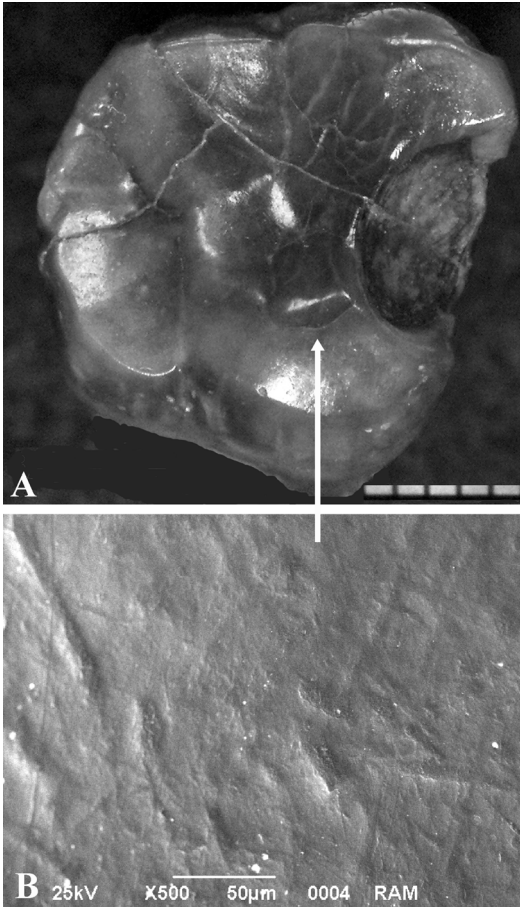
Fig. 9. (**A**) *Indopithecus* M^2 (HDI-1) (scale 5 mm), and (**B**) scanning electron micrograph of the Phase II wear.

Fig. 10. (**A**) *Sivaladapis nagrii* P_4 (Hari I-6) and (**B**) scanning electron micrograph of the Phase II wear facet.

The isotope profile of *Indopithecus* (Fig. 12) shows an apparent annual variation in $\delta^{18}O$ of ca. 3‰ with mean = –3.9‰; this range is attenuated from the primary "body water" range due to enamel maturation and sampling geometry (Passey & Cerling 2002). The actual range in $\delta^{18}O$ of body water for *Indopithecus* was certainly higher than the measured 3‰, but without additional constraints on enamel maturation, we cannot provide quantitative estimates. *Sivapithecus* from Siwaliks of Pakistan had high $\delta^{18}O$ values (mean ≈ –2.6‰), which was interpreted to mean that *Sivapithecus* obtained most of its water from enriched upper-canopy vegetation (Nelson 2007).

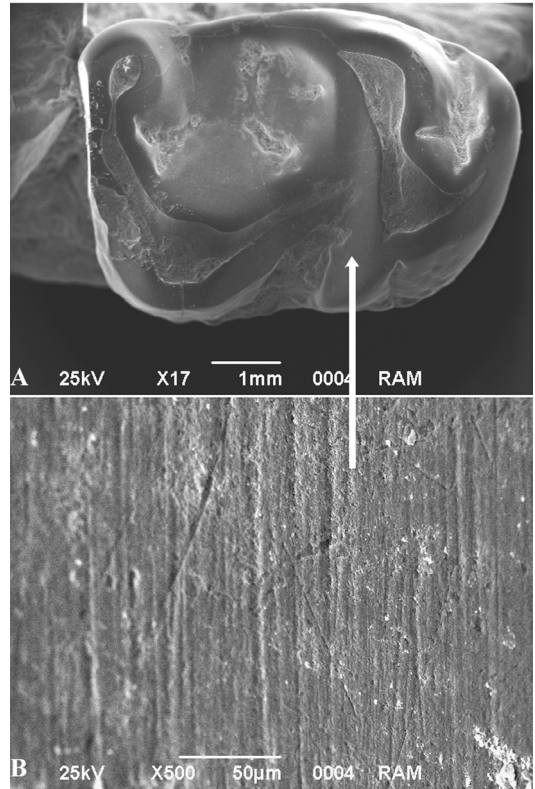Microwear study of the *Indopithecus* molar shown a high incidence of pits (58%) and a low percentage (42%) of mixed scratches; although most pits are small, a few of the pits are very wide and long (Fig. 9). Such a high pit percentage indicates frugivory, whereas presence of large pits similar to those found in extant baboons, such as *Papio*, may suggest reliance on fallback foods like hard seeds, nuts, barks and fruits with hard cover. Among the extinct apes, *Sivapithecus* comes closest to *Indopithecus* in having a large number of pits, some large pits and mixed scratches. The Phase II wear pattern of the Greek ape *Graecopithecus* (= *Ouranopithecus*) (*see* Merceron *et al.* 2005: fig. 3D) also shows striking resemblance to the texture seen in *Indopithecus*.

Indopithecus was a terrestrial giant ape that lived in a C_3-dominated habitat. Based on microwear and morphology, it is thought to have lived in a forested habitat. Its main food source might have been low-lying fruits. It might have also exploited other resources such as seeds, nuts, barks or even roots. Possible reliance on fallen
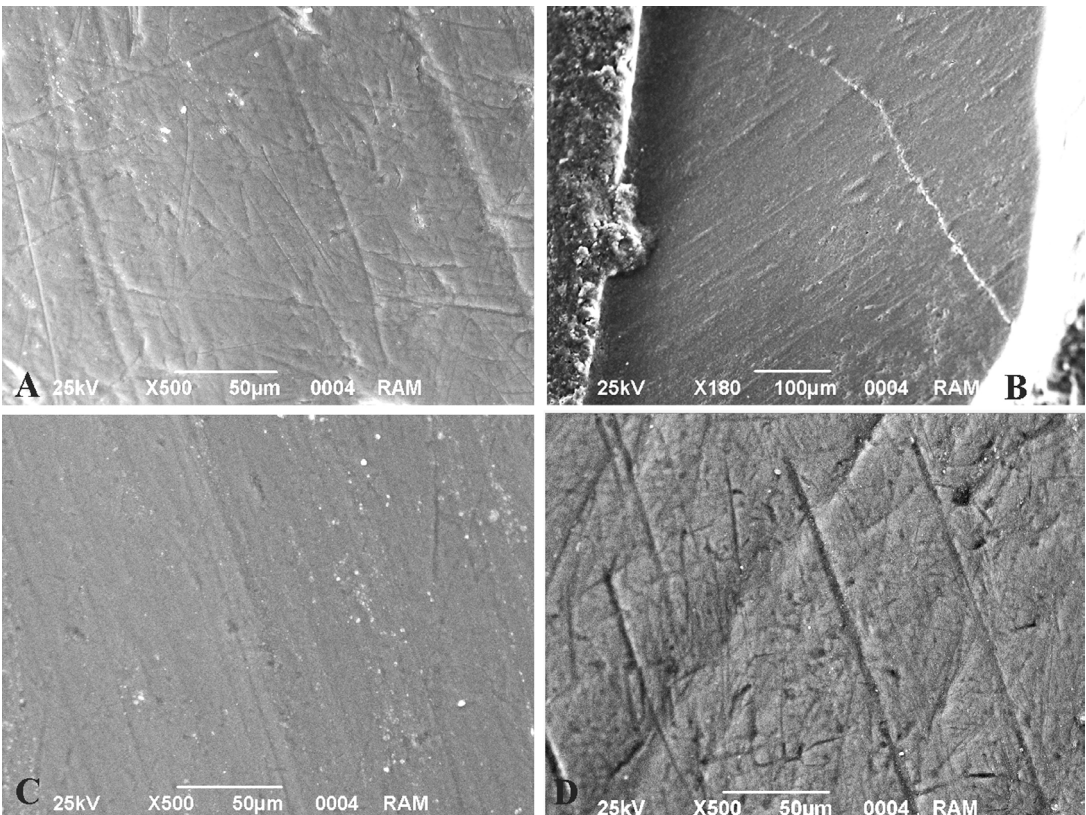
Fig. 11. Scanning electron micrograph of the Phase II wear facets of (**A**) *Sivalhippus* from Hari Devi site, (**B** and **C**) *Dorcatherium* molar from HT 1 site, and (**D**) *Theropithecus* (A643) molar from Mirzapur site.
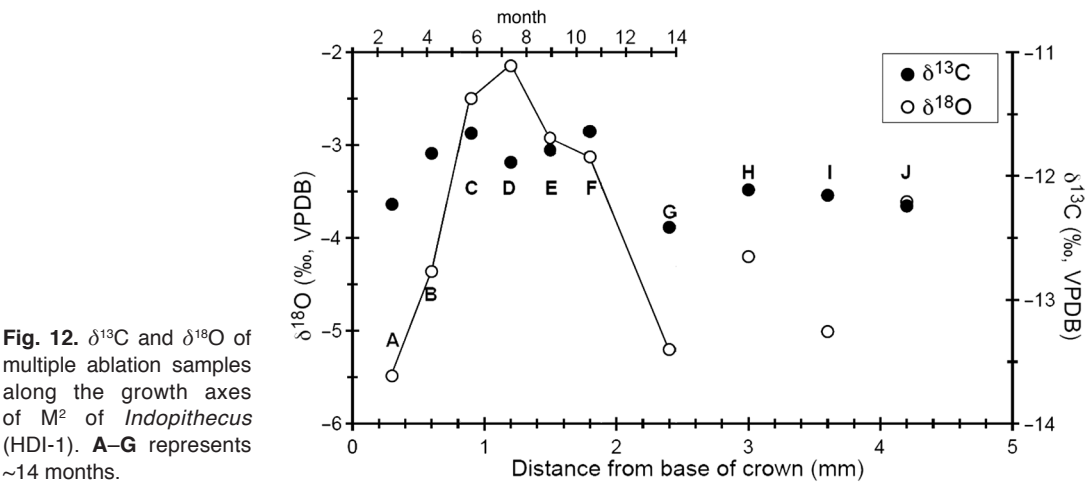

Fig. 12. $\delta^{13}C$ and $\delta^{18}O$ of multiple ablation samples along the growth axes of M² of *Indopithecus* (HDI-1). **A–G** represents ~14 months.

fruits and roots might explain presence of abrasive silica in its diet, which in turn would have produced wide scratches. However, its occasional reliance on bamboos or other C_3 grasses cannot be ruled out.

In earlier works it was hypothesized that *Indopithecus giganteus* (*Gigantopithecus bilaspurensis*) occupied an open country grassland landscape, which experienced aridity and seasonality (Simons & Chopra 1969, Pilbeam 1970,

Gaur & Vasishat 1989). The estimated enormous sizes of *Indopithecus* (150+ kg) and *Gigantopithecus blacki* (300 kg) suggest terrestrial locomotion in these giant apes (Fleagle 1999). Earlier microwear and phytolith studies on the Chinese specimens (*G. blacki*) are interpreted to indicate a diet of fruits and bamboos, and living in subtropical to tropical forest seasonal environments (Ciochon *et al*. 1990, Daegling & Grine 1994, Jablonski *et al*. 2000). A recent carbon isotope and enamel microwear study of *G. blacki* concluded that this giant ape had a pure C_3 diet and lived in a forested habitat; eight specimens of *Gigantopithecus blacki* yielded the $\delta^{13}C$ values between –13‰ and –16.8‰ (Zhao *et al*. 2011, Zhao & Zhang 2012). These highly ^{13}C-depleted values for *G. blacki* have been interpreted to indicate a close canopy forest habitat (following Cerling *et al*. 2004).

Sivaladapis

The estimated body-weight of *Sivaladapis* (3 kg) and its molar morphology indicates an ability to shear and puncture suggest folivory; *Sivaladapis nagrii* is interpreted as being an arboreal primate (Gingerich & Sahni 1984). White (2006) interpreted *Sivaladapis* as having a mixed frugivorous-folivorous diet.

The $\delta^{13}C$ values of *Sivaladapis nagrii* range between –11.3‰ and –14‰, indicating a pure C_3 diet. The range of the $\delta^{18}O$ values for associated fauna is very large (from ca. 0‰ to –12‰); the intermediate $\delta^{18}O$ value for *S. nagrii*, averaging –4.6‰, suggests that an evaporated source (e.g., leaves) was an important component of its water budget. This is seen in a $\delta^{13}C$ *vs*. $\delta^{18}O$ plot (*see* Fig. 8) of all the mammal enamel and soil carbonates coming from > 8 Ma. It is clear that overall the body water $\delta^{18}O$ values of the mammals, particularly those of the primates and bovids, were more enriched than the soil carbonate water values (Tables 2 and 3). *Indopithecus* and *Sivaladapis* are relatively enriched in $\delta^{18}O$ compared to most other fauna (Fig. 8).

The Phase II grinding wear facet microwear pattern (Fig. 10B) on *Sivaladapis nagrii* premolars and molars shows a high incidence of pits (~60%) and a low incidence of striations (~40%); most striations are fine and long, oriented parallel and close to each other, formed due to a sideways (labio-lingual) jaw movement. However, many striations are coarse; the presence of coarse striations could be due to feeding on leaves with large phytoliths or even C_3 grass (Mac Naughton *et al*. 1985, Ungar 1994). This characteristic pattern was observed in the trailing linear edges of lower pre-molars and molars of all the ca. 15 individuals examined. An abrasive diet is also evident from the prevalent exposure of the dentine due to the erosion of the thin enamel, in most of the specimens observed. This pattern implies that *Sivaladapis nagrii* was not a specialised folivore: rather it ate both fruits and leaves (White 2006). The tragulid *Dorcatherium* lower first molar from the *Sivaladapis* site (HT1) also shows a microwear pattern (Fig. 11B and C) that result from intake of some sort of abrasive diet as well, besides feeding on leaves and fruits. Obligate folivores such as *Gorilla* show similar parallel-oriented striations and a very low incidence of pits, but the striations are usually finer.

Soil carbonates and associated fauna from this time interval in the Dhok Pathan show a C_3-dominated ecosystem; as with *Indopithecus*, however, the relatively open nature of the habitat cannot be evaluated using stable isotopes because these fossils are older than the global C_4 expansion.

Sivaladapids became extinct in the late Miocene and *Sivaladapis nagrii* was the last Siwalik species to disappear. Its last known occurrence is at the site HT-1 of Haritalyangar dated to 9.1 Ma (Pillans *et al*. 2005, Patnaik 2013). Late Miocene climate change and biotic exchanges have been hypothesised to have influenced the primate diversity in Asia (Barry *et al*. 2002, Zheng *et al*. 2004, Patnaik *et al*. 2005). A contemporary of *Sivaladapis*, the Miocene ape *Sivapithecus* was thought to have disappeared because of the spread of grasslands and deterioration of rainforest habitat during the late Miocene (Patnaik *et al*. 2005, Nelson 2007). It has also been suggested that sivaladapids might have lost their ground due to competition from invading cercopithecoids that arrived from Africa in the late Miocene (Gingerich & Sahni 1979, 1984, Kirk & Simons 2001).

Theropithecus

The *Theropithecus delsoni* δ^{13}C and δ^{18}O values of –1.9‰, and –2.0‰, respectively, are indicative of a C_4 diet. The extant gelada is a graminivore and C_3 grazer, and is limited to high altitudes in Ethiopia above the altitudinal C_4–C_3-transition zone (ca. 2700 m; Tieszen *et al*. 1979). δ^{13}C values of Pleistocene *Theropithecus oswaldi* from eastern and southern Africa indicate a diet composed primarily of C_4 plants (Lee-Thorp *et al*. 1989, Lee-Thorp & van der Merwe 1993, Van der Merwe *et al*. 2003, Cerling *et al*. 2013).

Overall, the stable isotope values of other mammalian fossils collected from Mirzapur and surrounding areas indicate presence of grasslands during the Pleistocene time (Table 2). For instance, *Equus*, *Hipparion*, *Hemibos*, *Sivatherium*, *Camelus* and *Rhinoceros* have the δ^{13}C and δ^{18}O values indicating C_4 grazing under highly seasonal conditions. The *Hexaprotodon* δ^{13}C and δ^{18}O values indicate it was a highly water dependent C_4-grazer. Elephantids have both grazing and browsing to mixed-diet members: *Elephas* was a nearly pure C_4-grazer based on δ^{13}C values; the range of the δ^{13}C values for *Stegodon*, –7.3‰ to –11.7‰, permits only a minor fraction of C_4 plants in the diet and it is likely, therefore, that *Stegodon* was predominantly a C_3 browser.

Theropithecus microwear having a high incidence of long wide scratches and few pits also suggests grazing (Fig. 11D). The small mammalian assemblage from Pinjor Formation in general indicate presence of seasonal monsoonal climate (Patnaik 2003).

Conclusions

Laser ablation stable carbon and oxygen isotope analysis was carried out on the lateral enamel surface of an isolated tooth of *Indopithecus*, a Late Miocene Siwalik giant ape. An SEM-based counting of growth lines (perikymata) sampled, and the number of daily cross striations (11) each perikymata contained, permitted us to resolve the individual's diet and body water over a ca. 1-year period (Fig. 12). The *Indopithecus* enamel δ^{13}C values range between –12.4‰ and –11.6‰ (mean = –12‰), which indicate a pure C_3 diet. In view of the attenuation of the isotope signal due to maturation of enamel (Passey & Cerling 2002), an apparent intra-annual variation in δ^{18}O of ca. 3‰ may suggest a significant seasonality, comparable to present day monsoons (*see* Fig. 2). A dental enamel microwear study of *Indopithecus* molars show a high incidence (~60%) of pits similar to those found in dominantly frugivorous apes such as *Sivapithecus*. The presence of large pits and wide scratches on the molar of this giant ape, however suggest diet that included hard objects such as seeds, nuts, roots and fruits with hard cover.

The small primate *Sivaladapis nagrii* dental enamel δ^{13}C and δ^{18}O values (means being –12‰ and –4.6‰, respectively) and microwear showing both pits and striations suggest a C_3 diet comprised of leaves and fruits. However, the presence of coarse striations may indicate a diet of abrasive nature, not meant for its thin enamel.

All the taxa from ca. 8.8 to 10 Ma had C_3-dominated diets and paleosols from this time interval also indicate C_3-dominated ecosystems.

Stable carbon isotope and dental microwear data of *Theropithecus delsoni* reflect a primarily C_4 grass diet; in the Plio-Pleistocene, the associated ungulate fauna in the northwest Indian Siwaliks had strongly C_4-dominated diet except *Stegodon*, which had a C_3-dominated diet.

Acknowledgements

References

Barry, J. C., Morgan, M. E., Flynn, L. J., Pilbeam, D., Behrensmeyer, A. K., Raza, S. M., Khan, I. A., Badgley, C., Hicks, J. & Kelley, J. 2002: Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. — *Paleobiology Memoirs* 28(2) Supplement: 1–71.

Beard, K. C., Marivaux, L., Tun, S. T., Soe, A. N., Chaimanee, Y. A., Htoon, W., Marandat, B., Aung, H. H. & Jaeger, J.-J. 2007: New sivaladapid primates from the Eocene Pondaung Formation of Myanmar and the anthropoid status of Amphipithecidae. — *Bull. Carnegie Museum of Natural History* 39: 67–76.

Bocherens, H., Koch, P., Mariotti, A., Geraads, D. & Jaeger, J.-J. 1996: Isotopic biogeochemistry (^{13}C, ^{18}O) of mammalian enamel from African Pleistocene hominid sites. — *Palaios* 11: 306–318.

Brozovic, N. & Burbank, D. W. 2000: Dynamic fluvial systems and gravel progradation in the Himalayan foreland. — *Geological Society of America Bulletin* 112: 394–412.

Bryant, J., Luz, B. & Froelich, P. 1994: Oxygen isotopic composition of fossil horse tooth phosphate as a record of continental paleoclimate. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 107: 303–316.

Bryant, J., Froelich, P., Showers, W. & Genna, B. 1996: Biological and climatic signals in the oxygen isotopic composition of Eocene–Oligocene equid enamel phosphate. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 26: 75–89.

Cameron, D. W. 2001: The taxonomic status of the Siwalik Late Miocene hominid. *Gigantopithecus* ('*Indopithecus*'). — *Himalayan Geology* 22: 29–34.

Cameron, D. W. 2003: A functional and phylogenetic interpretation of the late Miocene Siwalik hominid *Indopithecus* and the Chinese Pleistocene hominid *Gigantopithecus*. — *Himalayan Geology* 24: 19–28.

Cerling, T. E. & Harris, J. M. 1999: Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. — *Oecologia* 120: 347–363.

Cerling, T. & Sharp, Z. 1996: Stable carbon and oxygen isotope analysis of fossil horse tooth enamel using laser ablation. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 126: 173–186.

Cerling, T. E., Harris, J. M., MacFadden, M. G., Leakey, M. G. & Quade, J. 1997: Global vegetation change through the Miocene/Pliocene boundary. — *Nature* 389: 153–158.

Cerling, T. E., Hart, J. A. & Hart, T. B. 2004: Stable isotope ecology in the Ituri Forest. — *Oecologia* 138: 5–12.

Cerling, T. E., Mbua, E., Kirera, F. M., Manthi, F. K., Grine, F. E., Leakey, M. G., Sponheimer, M. & Uno, K. T. 2011: Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. — *Proceedings of the National Academy of Sciences of the USA* 108: 9337–9341.

Cerling, T. E., Chitz, K. L., Jablonski, N. G., Leakey, M. G. & Manthi, F. K. 2013: Diet of *Theropithecus* from 4 to 1 Ma in Kenya. — *Proceedings of the National Academy of Sciences of the USA* 110: 10507–10512.

Chaimanee, Y., Yamee, C., Tian, P., Chavasseau, O. & Jaeger, J.-J. 2008: First middle Miocene sivaladapid primate from Thailand. — *Journal of Human Evolution* 54: 434–443.

Ciochon, R. L., Piperno, D. R. & Thompson, R. G. 1990: Opal phytoliths found on the teeth of *Gigantopithecus blacki*: implications for paleodietary studies. — *Proceedings of the National Academy of Sciences of the USA* 87: 8120–8124.

Daegling, D. J. & Grine, F. E. 1994: Bamboo feeding, dental microwear, and diet of the Pleistocene ape *Gigantopithecus blacki*. — *South African Journal of Science* 90: 527–532.

Daegling, D. V. & Grine, F. E. 1999: Terrestrial foraging and dental microwear in *Papio ursinus*. — *Primates* 40: 559–572.

Dansgaard, W. 1964: Stable isotopes in precipitation. — *Tellus* 16: 436–468.

Dean, M. C. 1987: Growth layers and incremental markings in hard tissues; a review of the literature and some preliminary observations about enamel structure in *Paranthropus boisei*. — *Journal of Human Evolution* 16: 157–172.

Dean, M. C. 1998: A comparative study of cross striation spacings in cuspal enamel and of four methods of estimating the time taken to grow molar cuspal enamel in *Pan*, *Pongo* and *Homo*. — *Journal of Human Evolution* 35: 449–462.

Dean, C. 2000: Progress in understanding hominoid dental development. — *Journal of Anatomy* 197: 77–101.

Dean, M. C. & Schrenk, F. 2003: Enamel thickness and development in a third permanent molar of *Gigantopithecus blacki*. — *Journal of Human Evolution* 45: 381–387.

Delson, E. 1993: *Theropithecus* fossils from Africa and India and the taxonomy of the genus. — In: Jablonski, N. G. (ed.), *Theropithecus: the rise and fall of a primate genus*: 157–189. Cambridge University Press, Cambridge.

Delson, E., Eck, G. G., Leakey, M. G. & Jablonski, N. G. 1993: A partial catalogue of fossil remains of *Theropithecus*. — In: Jablonski, N. G. (ed.), *Theropithecus: the rise and fall of a primate genus*: 499–525. Cambridge University Press, Cambridge.

Dirks, W. & Bowman, J. E. 2007: Life history theory and dental development in four species of catarrhine primates. — *Journal of Human Evolution* 53: 309–320.

Ducrocq, S., Jaeger, J.-J., Chaimanee, Y. & Suteethorn, V. 1995: New primate from the Paleogene of Thailand, and the biogeographical origin of anthropoids. — *Journal of Human Evolution* 28: 477–485.

El-Zaatari, S., Grine, F. E., Teaford, M. F. & Smith, H. F. 2005: Molar microwear and dietary reconstructions of fossil Cercopithecoidea from the Plio-Pleistocene deposits of South Africa. — *Journal of Human Evolution* 49: 180–205.

FitzGerald, C. M. 1998: Do enamel microstructures have regular time dependency? Conclusions from the literature and a large scale study. — *Journal of Human Evolution* 35: 371–386.

Fleagle, J. F. 1999: *Primate adaptation and evolution*, 2nd ed. — Academic Press, New York.

Fleagle, J. G., Shea, J. J., Grine, F. E., Baden, A. L. & Leakey, R. E. (eds.) 2010: *Out of Africa 1: the first colonization of Eurasia*. — Springer, Dordrecht.

Flynn, L. J. & Morgan, M. 2005: New lower primates from the Miocene Siwaliks of Pakistan. — In: Lieberman, D. E., Smith, R. J. & Kelley, J. (eds.), *Interpreting the past: essays on human, primate, and mammal evolution in honor of David Pilbeam*: 81–102. Brill Academic Publishers, Boston.

Fox, D. & Fisher, D. 2001: Stable isotope ecology of a Late Miocene population of *Gomphotherium productus* (Mammalia, Proboscidea) from Port of Entry Pit, Oklahoma, USA. — *Palaios* 16: 279–293.

Fricke, H. C. & O'Neil, J. R. 1996: Inter- and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel phosphate: implications for paleoclimatological and paleobiological research. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 126: 91–99.

Fricke, H. C., Clyde W. C., O'Neil, J. R. & Gingerich, P. D. 1998: Evidence for rapid climate change in North America during the latest Paleocene thermal maximum: oxygen isotope compositions of biogenic phosphate from the Bighorn Basin (Wyoming). — *Earth Planetary Science Letters* 60: 193–208.

Gadbury, C., Todd, L., Jahren, A. & Amundson, R. 2000: Spatial and temporal variations in the isotopic composition of bison tooth enamel from the Early Holocene Hudson-Meng Bone Bed, Nebraska. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 157: 79–93.

Gaur, R. & Vasishat, R. N. 1989: Hominid Palaeoecology of the Indian Siwaliks. — In: Sahni, A. & Gaur, R. (eds.), *Perspectives in human evolution*: 195–222. Renaissance Publishing House. New Delhi.

Gebo, D. L., Dagosto, M., Beard, K. C. & Wang, J. 1999: A first metatarsal of *Hoanghonius stehlini* from the Late Middle Eocene of Shanxi Province, China. — *Journal of Human Evolution* 37: 801–806.

Gelvin, B. R. 1980: Morphometric affinities of *Gigantopithecus*. — *American Journal of Physical Anthropology* 53: 541–568.

Gingerich, P. D. & Sahni, A. 1979: *Indraloris* and *Sivaladapis*: Miocene adapid primates from the Siwaliks of India and Pakistan. — *Nature* 279: 415–416.

Gingerich, P. D. & Sahni, A. 1984: Dentition of *Sivaladapis nagrii* (Adapidae) from the late Miocene of India. — *International Journal of Primatology* 5: 63–79.

Gingerich, P. D., Holroyd, P. A. & Ciochon, R. L. 1994: *Rencunius zhoui*, new primate from the late middle Eocene of Henan, China, and a comparison with some early Anthropoidea. — In: Fleagle, J. G. & Kay, R. F. (eds.), *Anthropoid origins*: 143–162. Plenum Press, New York.

Grine, F. E. & Kay, R. F. 1988: Early hominid diets from quantitative image analysis of dental microwear. — *Nature* 333: 765–768.

Grine, F. E., Teaford, M. F., Ungar, P. & El-Zaatari, S. 2009: Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. — *Journal of Human Evolution* 51: 297–319.

Gupta, V. J. & Sahni, A. 1981: *Theropithecus delsoni*, a new cercopithecine species from the upper Siwaliks of India. — *Bulletin Indian Geologist Association* 14: 69–71.

Hu, R., Zhao, L. X. & Wu, X. Z. 2011: Periodicity of Retzius lines in fossil *Pongo* from South China. — *Chinese Science Bulletin* 57: 790–794.

IAEA 1981: *World survey of isotope concentrations in precipitation*. — International Atomic Energy Agency, Vienna.

Jablonski, N. G., Whitfort, M. J., Roberts-Smith, N. & Xu, Q. 2000: The influence of life history and diet on the distribution of catarrhine primates during the Pleistocene in eastern Asia. — *Journal of Human Evolution* 39: 131–157.

Kay, R. F. 1975: The functional adaptations of primate molar teeth. — *American Journal of Physical Anthropology* 43: 195–215.

Kay, R. F. & Covert, H. H. 1984: Anatomy and behaviour of extinct primates. — In: Chivers, D. J., Wood, B. A. & Bilsborough, A. (eds.), *Food acquisition and processing in Primates*: 467–508. Plenum, New York.

Kim, S. T. & O'Neil, J. R. 1997: Equilibrium and non equilibrium oxygen isotope effects in synthetic carbonates. — *Geochimica et Cosmochimica Acta* 61: 3461–3475.

King, T., Andrews, P. & Boz, B. 1999: Effect of taphonomic processes on dental microwear. — *American Journal of Physical Anthropology* 108: 359–373.

Kirk, E. C. & Simons, E. L. 2001: Diets of fossil primates from the Fayum Depression of Egypt: a quantitative analysis of molar shearing. — *Journal of Human Evolution* 40: 203–229.

Koch, P. L., Fisher, D. C. & Dettman, D. 1989: Oxygen isotope variation in the tusks of extinct proboscideans: a measure of season of death and seasonality. — *Geology* 17: 515–519.

Kohn, M. J. 1996: Predicting animal $\delta^{18}O$: accounting for diet and physiological adaptation. — *Geochimica et Cosmochimica Acta* 60: 4811–4829.

Kohn, M. J., Schoeninger, M. J. & Valley, J. W. 1996: Herbivore tooth oxygen isotope compositions: effect of diet and physiology. — *Geochimica et Cosmochimica Acta* 60: 3889–3896.

Kumar, R., Ghosh, S. K., Sangode, S. J. & Thakur, V. C. 2002: Manifestation of intra-foreland thrusting in the Neogene Himalayan foreland basin fill. — *Journal of Geological Society of India* 59: 547–560.

Lee-Thorp, J. A. & van der Merwe, N. J. 1987: Carbon isotope analysis of fossil bone apatite. — *South African Journal of Science* 83: 712–715.

Lee-Thorp, J. A. & van der Merwe, N. J. 1993: Stable carbon isotope studies of Swartkrans fossils. — In: Brain, C. K. (ed.), *Swartkrans. A cave's chronicle of early man*: 251–256. Transvaal Museum Monograph.

Lee-Thorp, J. A., van der Merwe, N. J. & Brain, C. K. 1989: Isotopic evidence for dietary differences between two extinct baboon species from Swartkrans. — *Journal of Human Evolution* 18: 183–190.

Lewis, G. E. 1933: Preliminary notice of a new genus of lemuroid from the Siwaliks. — *American Journal of Sci-*

ence 26: 134–138.

Luz, B. & Kolodny, Y. 1985: Oxygen isotope variations in phosphates of biogenic apatites, IV: mammal teeth and bones. — *Earth and Planetary Science Letters* 75: 29–36.

MacNaughton, S. J., Tarrants, J. L., Mac Naughton, M. M. & Davis, R. H. 1985: Silica as a defence against herbivory and a growth promotor in African grasses. — *Ecology* 66: 528–535.

Mahoney, P., Smith, T. M. & Schwartz, G. T. 2007: Molar crown formation in the Late Miocene Asian hominoids, *Sivapithecus parvada* and *Sivapithecus indicus*. — *Journal of Human Evolution* 53: 61–68.

Marivaux, L., Welcomme, J.-L., Ducrocq, S. & Jaeger, J.-J. 2002: Oligocene sivaladapid primate from the Bugti Hills (Balochistan, Pakistan) bridges the gap between Eocene and Miocene adapiform communities in southern Asia. — *Journal of Human Evolution* 42: 379–388.

Martínez-Navarro, B. 2004: Hippos, pigs, bovids, sabertoothed tigers, monkeys and hominids dispersals during Late Pliocene and Early Pleistocene times through the Levantine Corridor. — In: Goren-Inbar, N. & Speth, J. D. (eds.), *Proceedings of the conference "Human Paleoecology in the Levantine Corridor"*: 37–51. Oxbow Books, Oxford.

Merceron, G., Blondel, C., Bonis, L. de, Koufos, G. D. & Viriot, L. 2005: A new method of dental microwear analysis: application to extant primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). — *Palaios* 20: 551–561.

Nelson, S. 2003: *The extinction of Sivapithecus: faunal and environmental changes in the Siwaliks of Pakistan*. — American School of Prehistoric Research Monographs vol. 1, Brill Academic Publishers, Boston.

Nelson, S. 2005: Paleoseasonality inferred from equid teeth and intra-tooth isotopic variability. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 222: 122–144.

Nelson, S. 2007: Isotopic reconstructions of habitat change surrounding the extinction of Sivapithecus, a Miocene hominoid, in the Siwalik Group of Pakistan. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 243: 204–222.

O'Grady, S. P., Remien, C. H., Wende, A. R., Valenzuela, L. O., Enright, L. E., Chesson, L. A., Abel, E. D., Cerling, T. E. & Ehleringer, J. R. 2010: Aberrant water homeostasis detected by stable isotope analysis. — *PLoS ONE,* 5(7): e11699, doi:10.1371/journal.pone.0011699.

O'Grady, S. P., Valenzuela, L. O., Remien, C. H., Enright, L. E., Jorgensen, M. J., Kaplan, J. D., Wagner, J. D., Cerling, T. E. & Ehleringer, J. R. 2012: Hydrogen and oxygen isotope ratios in body water and hair: modelling isotope dynamics in nonhuman primates. — *American Journal of Primatology* 74: 651–660.

Pan, Y. 1988: Small fossil primates from Lufeng, a latest Miocene site in Yunnan Province, China. — *Journal of Human Evolution* 17: 359–366.

Pan, Y. & Wu, R. 1986: A new species of *Sinoadapis* from the Lufeng hominoid locality. — *Acta Anthropologica Sinica* 5: 31–49.

Passey, B. H. & Cerling, T. E. 2002: Tooth enamel miner-

alization in ungulates; implications for recovering a primary isotopic time-series. — *Geochimica et Cosmochimica Acta* 66: 3225–3234.

Passey, B. H. & Cerling, T. E. 2006: In situ stable isotope analysis (δ^{13}C, δ^{18}O) of very small teeth using laser ablation GC/IRMS: — *Chemical Geology* 235: 238–249.

Passey, B. H., Robinson, T. F., Ayliffe, L. K., Cerling, T. E., Sponheimer, M., Dearing, M. D., Roeder, B. L. & Ehleringer, J. R. 2005: Carbon isotopic fractionation between diet, breath, and bioapatite in different mammals. — *Journal of Archaeological Science* 32: 1459–1470.

Passey, B. H., Cerling, T. E. & Levin, N. E. 2007: Temperature dependence of acid fractionation for modern and fossil tooth enamels. — *Rapid Communication. Mass Spectrometry* 21: 2853–2859.

Patnaik, R. 2003: Reconstruction of Upper Siwalik palaeoecology and palaeoclimatology using microfossil palaeocommunities. — *Palaeoecology, Palaeoclimatology Palaeogeography*197: 133–150.

Patnaik, R. 2013: Neogene Siwalik mammalian biostratigraphy: an overview. — In: Wang, X., Flynn, L. J. & Fortelius, M. (eds.), *Fossil mammals of Asia: Neogene biostratigraphy and chronology*: 423–444. Columbia University Press, New York.

Patnaik, R. & Nanda, A. C. 2010: Early Pleistocene mammalian faunas of India and evidence of connections with other parts of the world. — In: Fleagle, J., Shea, J. & Leakey, R. (eds.), *Out of Africa I: the first hominins of Eurasia*: 423–444. Paleobiology and Paleoanthropology Series, Springer, New York.

Patnaik, R., Cameron, D., Sharma, J. C. & Hogarth, J. 2005: Extinction of Siwalik fossil apes: a review based on a new fossil tooth and on palaeoecological and palaeoclimatological evidence. — *Anthropological Science* 113: 65–72.

Pilbeam, D. 1970: *Gigantopithecus* and the origins of hominidae. — *Nature* 225: 516–519.

Pilgrim, G. E. 1915: The New Siwalik Primates and their bearing on the question on the origin of man and Anthropoidea. — *Records of Geological Survey of India* 45: 1–74.

Pillans, B., Williams, M., Cameron, D., Patnaik, R., Hogarth, J., Sahni, A., Sharma, J. C., Williams, F. & Bernor, R. 2005: Revised correlation of the Haritalyangar magnetostratigraphy, Indian Siwaliks: implications for the age of the Miocene hominids *Indopithecus* and *Sivapithecus*, with a note on a new hominid tooth. — *Journal of Human Evolution* 48: 507–515.

Podlesak, D. W., Torregrossa, A. M., Ehleringer, J. R., Dearing, M. D., Passey, B. H. & Cerling, T. E. 2008: Turnover of oxygen and hydrogen isotopes in the body water, CO_2, hair and enamel of a small mammal after a change in drinking water. — *Geochimica et Cosmochimica Acta* 72: 19–35.

Podlesak, D. W., Bowen, G. J., O'Grady, S., Cerling T. E. & Ehleringer, J. R. 2012: δ^2H and δ^{18}O of human body water: a GIS model to distinguish residents from nonresidents in the contiguous USA. — *Isotopes in Environmental and Health Studies* 48: 259–279.

Prasad, K. N. 1970: The vertebrate fauna from the Siwalik

beds of Haritalyangar, Himachal Pradesh, India. — *Memoirs of the Geological Society of India — Palaeontologica India* 39: 1–55.

Qi, T. & Beard, K. C. 1998: Late Eocene sivaladapid primate from Guangxi Zhuang Autonomous Region, People's Republic of China. — *Journal of Human Evolution* 35: 211–220.

Quade, J. & Cerling, T. E. 1995: Expansion of C$_4$ grasslands in the Late Miocene of northern Pakistan — evidence from stable isotopes in paleosols. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 115: 91–116.

Rafferty, K. L., Teaford, M. F. & Jungers, W. L. 2002: Molar microwear of subfossil lemurs: improving the resolution of dietary inferences. — *Journal of Human Evolution* 43: 645–657.

Ramdarshan, A., Merceron, G., Tafforeau, P. & Marivaux, L. 2010: Dietary reconstruction of the Amphipithecidae (Primates, Anthropoidea) from the Paleogene of South Asia and paleoecological implications. — *Journal of Human Evolution* 59: 96–108.

Reid, D. J., Ferrell, R. & Walton, P. 2002: Histological of dental derived canine crown formation times from a medieval Danish sample. — *American Journal of Physical Anthropology* 34 (Suppl): 129.

Rook, L., Martinez-Navarro, B. & Howell, F. C. 2004: Occurrence of *Theropithecus* sp. in the Late Villafranchian of southern Italy and implication for Early Pleistocene "out of Africa" dispersals. — *Journal of Human Evolution* 47: 267–277.

Sahni, A. 1989: Siwalik adapid primates: taxonomy, distribution, and enamel ultrastructure. — In: Sahni, A. & Gaur, R. (eds.), *Perspectives in human evolution: S.R.K. Chopra Festschrift Volume*: 173–187. Renaissance Publishing House, Delhi.

Sahni, M. R. & Khan, E. 1964: Stratigraphy, structure and correlationof the Upper Shivaliks east of Chandigarh. — *Journal of the Palaeontological Society of India* 4: 61–74.

Schwartz, G. T., Reid, D. & Dean, C. 2001: Developmental aspects of sexual dimorphism in hominoid canines. — *International Journal of Primatology* 22: 837–860.

Sharp, Z. & Cerling, T. E. 1998: Fossil isotope records of seasonal climate and ecology: straight from the horse's mouth. — *Geology* 26: 219–222.

Simons, E. L. & Chopra, S. R. K. 1969: *Gigantopithecus* (Pongidae, Hominoidea): a new species from northern India. — *Postilla* 138: 1–8.

Simons, E. L. & Pilbeam, D. 1965: Preliminary revision of Dryopithecinae (Pongidae, Anthropoidae). — *Folia Primatologia* 3: 1–152.

Smith, T. M., Dean, M. C., Kelley, J., Martin, L. B., Reid, D. J. & Schwartz, G. T. 2003: Molar crown formation in Miocene hominoids: a preliminary synthesis. — *American Journal of Physical Anthropology* 36: 196.

Smith, T. M., Martin, L. B., Reid, D. J., de Bonis, L. & Koufos, G. D. 2004: An examination of dental development in *Graecopithecus freybergi* (*Ouranopithecus macedoniensis*). — *Journal of Human Evolution* 46: 551–577.

Sponheimer, M. & Lee-Thorpe, J. A. 1999: Isotopic evidence for the diet of a nearly hominid, *Australopithecus africanus*. — *Science* 283: 368–370.

Szalay, F. S. & Delson, E. 1979: *Evolutionary history of the primates*. — Academic Press, New York.

Tattersall, I. 1968: A mandible of *Indraloris* (Primates, Lorsidae) from the Miocene of India. — *Postilla* 123: 1–10.

Teaford, M. F. 1986: Dental microwear and diet in two species of Colobus. — In: Else, J. & Lee, P. (eds.), *Primate ecology and conservation*: 63–66. Cambridge University Press, Cambridge.

Teaford, M. F. & Glander, K. E. 1996: Dental microwear in a wild population ofmantled howlers (*Alouatta palliata*). — In: Norconk, M., Rosenberger, A. & Garber, P. (eds.), *Adaptive Radiations of Neotropical Primates*: 433–449. Plenum, New York.

Teaford, M. F. & Oyen, D. 1989: *In vivo* and *in vitro* turnover in dental microwear. — *American Journal of Physical Anthropolology* 80: 447–460.

Teaford, M. F. & Robinson, J. G. 1989: Seasonal or ecological zone differences in diet and molar microwear in *Cebus nigrivittatus*. — *American Journal of Physical Anthropolology* 80: 391–401.

Teaford, M. F. & Walker, A. C. 1984: Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. — *American Journal of Physical Anthropolology* 64: 191–200.

Thomas, H. & Verma, S. N. 1979: Découverte d'un primate adapiforme (Sivaladapinae sub fam. nov.) dans le Miocéne moyen des Siwaliks de la région de Ramnagar (Jammu et Cachemire, Inde). — *Comptes Rendus Academie Sciences* 289: 833–836.

Tieszen, L. L., Senyimba, M. M., Imbamba, S. K. & Troughton, J. H. 1979: The distribution of C$_3$ and C$_4$ grasses along an altitudinal and moisture gradient in Kenya. — *Oecologia* 37: 337–350.

Tong, Y. 1997: Middle Eocene small mammals from Linguanqiao Basin of Henan Province and Yuanqu Basin of Shanxi Province, central China. — *Paleontologica Sinica* 18: 189–256.

Tong Y. S., Wang, J. W. & Huang, X. S. 1999: Discovery of a nearly complete lower jaw of *Hoanghonius stehlini* Zdansky, 1930 (Mammalia, Primates). — *Vertebrata Palasiatica* 37: 105–119.

Ungar, P. S. 1994: Incisor microwear of Sumatran anthropoidprimates. — *American Journal of Physical Anthropolology* 94: 339–363.

Ungar, P. S. 1996: Dental microwear of European Miocene catarrhines: evidence for diets and tooth use. — *Journal of Human Evolution* 31: 355–366.

Ungar, P. S. 2002: *Microware software, version 4.0.2. A semi-automated image analysis system for the quantification of dental microwear*. — Fayetteville, AR.

Ungar, P. S., Grine, F. E., Teaford, M. F. & El-Zaatari, S. 2006: Dental microwearand diets of African early *Homo*. — *Journal of Human Evolution* 50: 78–95.

Ungar, P. S., Scott, R. S., Scott, J. R. & Teaford, M. F. 2008: Dental microwear analysis: historical perspectives and new approaches. — In: Irish, J. D. & Nelson, G. C. (eds.), *Volume on dental anthropology*: 389–425. Cam-

bridge University, Cambridge.

Van der Merwe, N. J., Thackeray, J. F., Lee-Thorp, J. A. & Luyt, J. 2003: The carbon isotope ecology and diet of Australopithecus africanus at Sterkfontein, South Africa. — *Journal of Human Evolution* 44: 581–597.

Von Koenigswald, G. H. R. 1950: Bemerkungen zu *Dryopithecus giganteus* Pilgrim. — *Eclogae Geologicae Helvetiae* 42: 515–519.

Walker, A. C. & Teaford, M. F. 1989: Inferences from quantitative analysis of dental microwear. — *Folia Primatologia* 53: 177–189.

White, J. 2006: Evolution of adapiform ecological diversity: a geometric morphometric analysis of molar occlusal surface shape. — *Journal of Vertebrate Paleontology* 26 (Suppl. 3): 138A.

Wolpoff, W. H. 1999: *Palaeoanthropology*, 2nd ed. — McGrawHill, Boston.

Woo, J. K. & Chow, M. C. 1957: New materials of the earliest primate known in China. — *Vertebrata Palasiatica* 1: 267–273.

Wu, R. & Pan, Y. 1985: A new adapid genus from the Miocene of Lufeng. — *Acta Anthropologica Sinica* 4: 1–6.

Zhao, L. X. & Zhang, L. Z. 2012: New fossil evidence and diet analysis of *Gigantopithecus blacki* and its distribution and extinction in South China. — *Quaternary International* 258: 69–74.

Zhao, L. X., Zhang, L. Z., Zhang, F. S. & Wu, X. Z. 2011: Enamel carbon isotope evidence of diet and habitat of *Gigantopithecus blacki* and associated mammalian megafauna in the Early Pleistocene of South China. — *Chinese Science Bulletin* 56: 3590–3595.

Zheng, H., Powell, C. M., Rea, D., Wang, J. & Wang, P. 2004: Late Miocene and mid-Pliocene enhancement of the east Asian monsoon as viewed from land and sea. — *Global and Planetary Change* 41: 147–155.